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Factors Affecting the Sensory Response Characteristics of the Cephalopod Statocyst and their Relevance in Predicting Swimming Performance

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Abstract. The statocyst in cephalopods is the main organ of balance and operates in a manner similar to the vestibular system of vertebrates. This paper reviews the principal factors affecting the sensitivity and frequency response of the statocyst. These include morphological features, such as the size and shape of the statocyst, its canal structure, and the size of the cupulae and maculae, as well as physiological features, such as the electrotonic coupling of sensory cells, the impact of the efferents, and the motility of some cells. The use of statocyst characteristics in predicting the locomotory performance of different cephalopod species is discussed.

Introduction

For spatial control of locomotion, an animal needs information about its orientation with respect to gravity and its motion relative to its surroundings. This information could be derived from a variety of sensory systems, ranging from vision to electroreception, but most animals have developed specific sense organs responding to linear and angular accelerations; *e.g.*, the vestibular system in vertebrates and the statocysts of cephalopods. It has been proposed that the sensory response characteristics of these receptor systems are matched to their likely inputs; *i.e.*, that the frequency response range and sensitivity of the system reflect the accelerations imposed by an animal's own movements (Jones and Spells, 1963; Jones, 1984). Thus the vestibular system of a small agile animal (*e.g.*, a bird) is more sensitive to higher frequencies of movement than that of a slower moving animal living in a denser medium (*e.g.*, a fish) (Correia *et al.*, 1981). This idea can also be applied to cephalopods where, by looking at the statocysts, we can try to predict what kind of locomotion is used by the animal (Maddock and Young, 1984; Morris, 1988; Young, 1989). This is a particularly valuable approach to animals with unstudied lifestyles. This paper reviews some of the evidence for this proposition and identifies some of the features that are likely to influence the sensitivity and response characteristics of cephalopod statocysts.

The parameters affecting statocyst sensitivity can be divided into two main areas, morphological features and physiological features. For convenience these are considered separately, but of course, they act in concert within the living animal.

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Morphological Features

The general morphology of each of the paired right and left statocysts is a fluid-filled cavity within the cranial cartilage (Fig. 1). The statocyst itself varies considerably in shape in different cephalopods; in *Octopus* (Fig. 1A) it is almost spherical, whereas in *Vampyroteuthis* it is short, wide, and shallow (Young, 1960, 1989). Many statocysts have sac-like protrusions into the surrounding cartilage (Stephens and Young, 1982), or cartilaginous pegs or hooks (the anticristae and hamuli) that project into the statocyst interior (Fig. 1B); these projections presumably constrict or direct the flow of the endolymph. Again, this can vary from the single anticrista in *Octopus*, to the 38 anticristae and 5 hamuli in *Egea* (Young, 1984).

Each statocyst has two main areas of receptor epithelium (Fig. 1). The first is a macula or plate of sensory hair cells with an overlying statolith. All coleoids have a macula carrying a single compact statolith, but decapods have two additional maculae carrying numerous small statoconia. Where three maculae are present, they are set in different planes, thus being able to resolve linear accelerations in any direction.

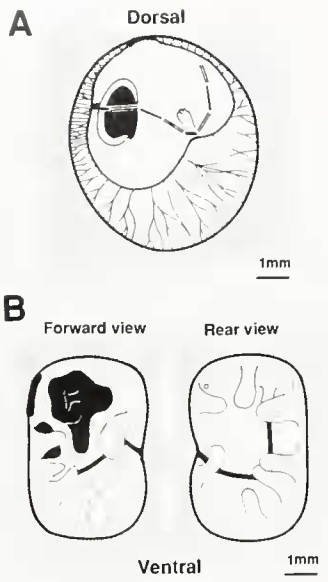

Figure 1. (A) Diagram of the statocyst of *Octopus* viewed from the side. The statocyst sac is suspended within the statocyst cavity by fibrous strands. There are two areas of receptor epithelium: a single, oval shaped macula with an attached statolith, and a crista strip that passes around the inside of the sac, such that it covers all three planes. The crista strip is divided into 9 segments, each segment carries a cupula (not shown). After Budelmann, 1980. (B) A forward and rear view of the cut open statocyst of *Sepia officinalis*. There are 3 maculae, arranged in 3 different planes, and the crista strip is divided into 4 segments. Anticristae and hamuli project into the cavity of the statocyst. After Budelmann, 1980.

The second area of receptor epithelium consists of a narrow strip of sensory hair cells that runs around the inside of the statocyst such that it covers all three planes (Fig. 1). This strip is usually divided into segments: the crista segments, each carrying a cupula attached along the length of the crista segment. Octopods (excluding cirroctopods) have nine crista segments, whereas decapods have four, each with its own cupula. Rotational movements of the animal cause a flow of endolymph relative to the statocyst wall; this flow in turn deflects the cupula and stimulates the underlying hair cells. A transverse section through a crista segment (Fig. 2) reveals three main types of cells in the sensory epithelium: primary sensory hair cells, secondary sensory hair cells, and afferent neurons. This combination of primary sensory hair cells and secondary sensory hair cells in a single epithelium is unique to cephalopods (Budelmann *et al.*, 1987). Although the crista/cupula system responds principally to angular accelerations, it may also respond to linear accelerations (Budelmann and Wolff, 1973; Williamson and Budelmann, 1985a). Because the crista/cupula system is crucial for signalling most of the animal's movements, and because this system is dependent upon the physical parameters of the statocyst, we will concentrate on the responses of the crista.

Statocyst size and shape

The idea that the size and shape of the statocyst are correlated with its likely response characteristics, and hence with the animal's locomotory performance, arises from the physical models of the operation of the vertebrate semicircular canal system (Steinhausen, 1933; Wilson and Jones, 1979) and from comparisons of canal dimensions in different animals (Jones and Spells, 1963; Jones, 1984; Gauldie and Radtke, 1990) and in animals of different sizes (Curthoys, 1983). The Steinhausen torsion pendulum model (Steinhausen, 1933; Oman *et al.*, 1987) identifies the radius of curvature of the canal, the bore radius of the canal duct, the viscosity and density of the endolymph, and the stiffness of the cupula as being important factors determining the vestibular response characteristics. Although, in vertebrates, there is a good correlation between the frequency sensitivity predicted from measurements of the radius of curvature of the canal and the bore radius of canal duct, and the actual response characteristics (Correia *et al.*, 1981), the statocyst position is much less clear.

The use of such a model in cephalopods is supported by the relatively large size of the statocysts in newly hatched coleoids. Those statocysts are more than a quarter of the mantle length, but grow at a much lower rate than the animal; *i.e.*, they increase in size by about 29 times while the mantle length is increasing by 390 times (Maddock and Young, 1984). This relative conservation of statocyst size fits well with the idea that statocyst size is constrained by the physical principles under which the organ operates, and that the dimensions of the system are adjusted to the speed at which the animal turns. In addition, Maddock and Young (Maddock and Young, 1984; Young, 1984, 1989) have described a number of correlations between statocyst morphology and probable swimming performance, including data showing that the faster moving squids tend to have a narrower canal, thus

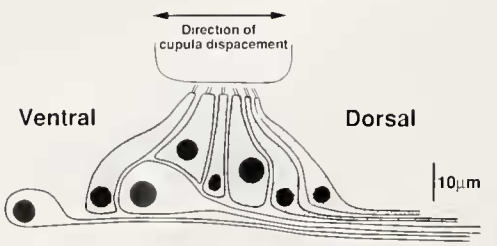

Figure 2. Diagram of a cross-section through the crista strip of the squid, *Alloteuthis subulata*. Three main cell types are present: the primary sensory hair cells (lightly stippled), the secondary sensory hair cells (darkly stippled), and the afferent neurons (unstippled). After Williamson, 1989a.

presumably improving the high frequency response, whereas slow moving cephalopods tend to have relatively large statocysts, thus increasing their low frequency sensitivity.

As pointed out by Young (1984), the main difficulties in applying this idea to cephalopod statocysts is that the radius of curvature can only be approximated as the cross-sectional diameter of the statocyst, and there is only rarely a canal-like structure in the statocyst formed by the anticrista and hamuli. In addition, although there are recognizable patterns of anticristae and hamuli in different groups of cephalopods, it is unclear how these projections affect the flow of endolymph. Clearly, we need a more realistic model of how the endolymph flows within the statocyst, and how this is influenced by the various morphological features of the statocyst.

Cupula parameters

Other morphological features likely to effect the frequency response and sensitivity of the statocyst angular acceleration receptor system are the size, shape, and attachment of the cupulae. The cupulae are gelatinous, flap-like structures, projecting towards the middle of the statocyst, and attached to the crista ridge along the whole length of a segment. The cupulae however, appear to be irregular in shape, often being much taller in the center of the crista segment than at the edges; this is particularly prominent in the squid, *Alloteuthis* (Fig. 3a). The center of the cupula will therefore present a much greater area of resistance to endolymph flow than the edges and hence, unless the cupula is very rigid, will more easily stimulate the underlying hair cells. This likely differential sensitivity in different parts of a single crista segment may be a method of fractionating the sensitivity range of the system. In *Octopus* this is even more pronounced (Fig. 3b,c). Here, the nine crista segments have alternating large and small cupulae, with the tall cupulae having narrower bases than the small ones (Budelmann *et al.*, 1987). This, again, is likely to fractionate the range over which the system operates and, indeed, recordings from the afferent neurons in representatives of these two different segments indicate that the segment with the large cupula is up to 10 times more sensitive than that with the small cupula (Williamson and Budelmann, 1985a,b). The increase in sensitivity means, however, that the afferents from the large segment can be driven into response saturation at a much lower stimulus intensity than those from the small cupula segment. This arrangement could be correlated with *Octopus'* two forms of locomotion, the high sensitivity, large cupulae being needed during slow crawling movements, and the low sensitivity, small cupulae during jet propelled movements.

Like the statoliths, anticristae, and hamuli, the cupulae are also likely to have an effect on the pattern of endolymph flow within the statocyst. Although Young (Maddock and Young, 1984; Young, 1989) has used a vertebrate semicircular canal model to predict endolymph flow, and hence sensory response characteristics, this is unlikely to be adequate. Recent vertebrate models have shown that even a good canal structure, with the three canals orthogonally arranged, is likely to have a complicated pattern of endolymph flow with crosstalk between the canals (Oman *et al.*, 1987; Muller and Verhagen, 1988). In cephalopods, which rarely have a single canal structure, endolymph flow patterns are extraordinarily difficult to predict (Govardovskii, 1971; Muller, pers. comm.). Even the manner of movement of the cupula is unknown; *i.e.*, whether it pivots like a lever, or slides like a piston, or flexes like a diaphram, although recent modelling work has suggested that the cupula does not operate as a simple pivot (Morris, 1988).

Another unknown with respect to cupula movement is the strength of its attachment to the crista and the restoring force it develops when displaced. This will have a

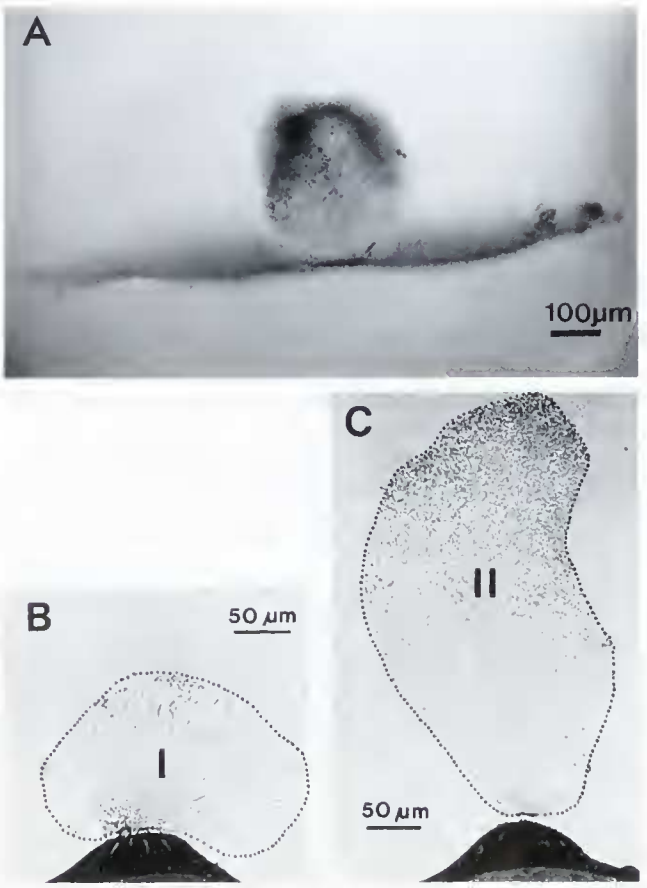

Figure 3. (A) Crista cupula from the squid, *Alloteuthis subulata*. The cupula has been fixed in osmium and then detached from the crista segment. Note that it has a large central mass and is much shorter at the edges. From Williamson 1990a. (B and C) Transverse sections through two different crista segments in the statocyst of *Octopus* showing a small, wide-based cupula type and a large, narrow-based cupula type. From Williamson and Budelmann, 1985b.

major impact on the frequency response characteristics of the crista/cupula system, and any variation between crista segments, or between different animals, would have to be taken into account in a model describing statocyst response characteristics.

The presence or absence of a perilymphatic space may also affect the sensitivity of the statocyst. The octopods, cirroctopods, and *Vampyroteuthis* all have a lymph-filled space between the cartilaginous wall of the statocyst cavity and the statocyst sac containing the sensory epithelia. Anliker and van Buskirk (1971), dealing with the vertebrate semicircular canal system, have argued that the movement of perilymph may have a major effect on the dynamic response characteristics of the system. Although any perilymph flow in the statocyst would be restricted by the fibers supporting the statocyst sac, there may well be an effect in cephalopods from this source.

Physiological Features

Extracellular recordings from statocyst afferents have shown that the crista/cupula system in *Octopus* acts as a velocity transducer over a middle range of frequencies and has response characteristics similar to those of the vertebrate semicircular canal system (Williamson and Budelmann, 1985a). There is as yet no data on afferent response characteristics from decapod statocysts. Recent intracellular recordings from hair cells in the statocyst of the squid, *Alloteuthis subulata*, have provided the first measurements of the sensitivities of cephalopod hair cells (Williamson, 1991a). This work (Fig. 4) has shown that the secondary sensory hair cells in the crista have sensitivities of at least 0.5 mV per degree of cilia deflection. This compares with sensitivities of about 3 mV per degree for frog saccular hair cells (Hudspeth and Corey, 1977), 10 mV per degree for turtle basilar papillar hair cells (Crawford and Fettiplace, 1985), and 30 mV per degree for mouse cochlear hair cells (Russell *et al.*, 1986). This work has also confirmed morphological studies (Budelmann *et al.*, 1987) showing that at least some of the secondary hair cells are physiologically polarized in the opposite direction to the primary hair cells (Fig. 4). This bipolar sensitivity does not occur in vertebrate vestibular cristae and, although it may be more energy efficient (Williamson, 1991a), it is not clear if it will have any effect on the sensitivity or frequency bandwidth of the system.

Differences in hair cell sensitivity

There may well be differences in the intrinsic sensitivities of the individual crista hair cells. In *Octopus*, there are at least three different morphological types of crista hair cells: the primary sensory hair cells, the small secondary sensory hair cells, and the large secondary sensory hair cells. In addition, there are different types of afferent

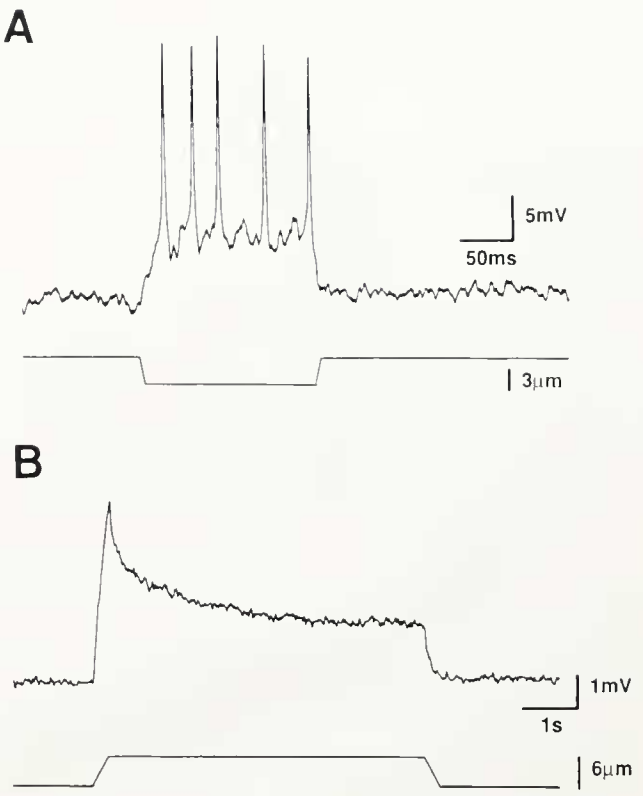

Figure 4. Intracellular recordings from a primary sensory hair cell (A) and a secondary sensory hair cell (B) in the crista of the squid statocyst, showing their responses to small mechanical displacements of the overlying cupula (displacements shown in lower traces). Note that the primary and secondary hair cell depolarizations are caused by cupula displacements of opposite directions, indicating that the cells are polarized in opposing directions, and that only the primary hair cell carries action potentials. From Williamson, 1991a.

neurons, and there may also be subdivisions of the hair cells types (Budelmann *et al.*, 1987). These morphological differences are likely to be reflected in physiological cell parameters, such as input impedance and cell conductance, and therefore result in differences in the sensitivities of the various cell types (Williamson and Budelmann, 1985a).

Electrical coupling

At least some of the secondary sensory hair cells in the squid statocyst cristae are known to be electrically coupled along the length of the crista segment (Fig. 5) (Williamson, 1989a). It has been argued that this coupling will lead to an improvement in the signal to noise ratio of the system and hence enhance its overall sensitivity. However, such coupling is also likely to lower the high frequency response of the system. Clearly, if the coupling could be varied under direct nervous control, this would be a powerful mechanism for changing the sensitivity and frequency response of the system. A comparable sensory system with

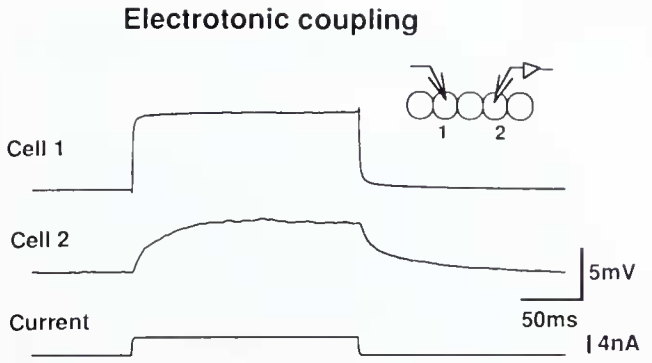

Figure 5. Intracellular recordings from two nearby secondary sensory hair cells in the statocyst crista of the cuttlefish, *Sepia officinalis*, showing their electrotonic coupling. A small current (bottom trace) is injected into Cell 1 (top trace), producing a depolarization, and this causes a simultaneous, but smaller, depolarization in the neighboring cells (Cell 2, middle trace). This provides evidence that the secondary sensory hair cells in a crista segment are electrotonically coupled along the segment. From Williamson, 1991b.

neurally controlled electrical coupling is in the vertebrate retina, where the neurotransmitter dopamine alters the coupling ratio between retinal horizontal cells (Knapp and Dowling, 1987). Dopamine has been located in the retinal efferents in *Octopus* (Suzuki and Tasaki, 1983) and has also been tentatively identified in the statocyst efferents (Budelmann and Bonn, 1982; Williamson, 1989b). It would be an astonishing example of parallel evolution if these two disparate sense organs, the eye and the statocyst, used dopaminergic control of electrical coupling to regulate their sensory input.

Efferent system

The statocysts have an exceptionally large efferent innervation; of the axons in the *Octopus* statocyst crista nerves, 75% are efferent fibers travelling from the brain to the statocyst (Budelmann *et al.*, 1987). In contrast, about 8% of axons in a vertebrate vestibular nerve are efferents (Goldberg and Fernandez, 1980). This efferent innervation forms a plexus running beneath the crista epithelium and makes synaptic contact with primary and secondary sensory hair cells, as well as with the afferent and other efferent neurons (Budelmann *et al.*, 1987). The efferent fibers are active during movements of the animal's head (Williamson, 1986) and can depress or enhance (Fig. 6) the afferent output from the statocyst (Williamson, 1985). These effects are due to direct synaptic hyperpolarization, or to depolarization, of the secondary sensory hair cells, their first-order afferent neurons, and possibly, the primary sensory hair cells (Williamson, 1989c). The inhibitory response is probably due to cholinergic synapses (Auerbach and Budelmann, 1986; Williamson, 1989b), and the excitatory response to catecholaminergic synapses (Budelmann and Bonn, 1982; Williamson, 1989b).

Such a widespread and complex efferent innervation provides the animal with direct and independent control of both the hair cell receptor potential and the level of activity of the afferent neurons. Thus, not only can the gain of the overall system be increased or decreased, but the responses of individual elements can also be varied. This permits an extension of the dynamic range of the system by allowing adjustments to the membrane potentials of the hair cells and afferent neurons, so that the cells' responses are maintained within their operating ranges and at their maximum sensitivities.

Motile cilia and cells

Another feature that may have an impact on the sensitivity of the statocyst hair cells is the presence of motile cilia. Ciliated cells are distributed all over the inner surface of the statocyst, as well as in Kölliker's canal (Young, 1960); these cells have beating cilia that set up minute endolymph currents within the statocyst (Budelmann, 1990). The biological significance of these cells is not clear, but the fluid flow that they produce may be sufficient to increase the background noise within the system and thus reduce the overall sensitivity of the receptor system.

In addition to these ciliated cells, which are motile, some of the sensory hair cells within the crista or macula epithelia may also have a motor capability. Sensory cells with motile beating cilia are present in the statocysts of other mollusks (Stommel *et al.*, 1980), and some circum-

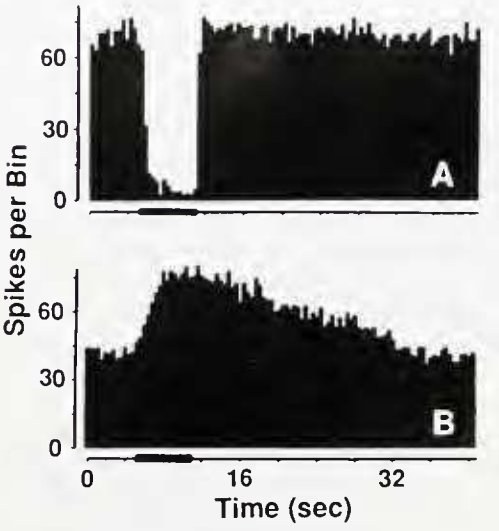

Figure 6. Peristimulus time histograms showing the effect of efferent activity on the statocyst afferent activity. Extracellular recordings were obtained from afferent neurons from the *Octopus* crista and then efferents to this segment activated by electrical stimulation (duration and time indicated by heavy bar on time axes). This caused an inhibition of the activity of unit A, but an increase in the activity of unit B. This provides evidence that there are both inhibitory and excitatory efferents innervating the statocyst crista. Bin width, 400 ms; stimulus, 50 Hz pulses for 6 s. From Williamson, 1985.

stantial evidence suggests that part of the membrane potential noise in recordings from some secondary sensory hair cells in squid crista may be due to ciliary movement (Williamson, 1991a). If some of the hair cells in the crista or macula do have a motor capability, this could have a large impact on the responses of the system. Recent work on vertebrate hair cells has shown that motility in the outer hair cells of the cochlea can change the response characteristics of the sensory system by altering the micromechanics of the basilar membrane responses (Hudspeth, 1989). This is thought to be due to changes in the length of the cells rather than an active beating of their cilia. Such a system, operating under efferent control, could also be present in the cephalopod statocyst.

Central processing

A final feature that can influence the characteristics of the statocyst input is the central processing of the statocyst information. This has two major functions: first, the central control of the statocyst efferents, and second, the analytical processing of the statocyst afferent information.

As has already been discussed, the efferents can have a major impact on the response characteristics of the statocyst. This can operate through a variety of mechanisms. In a feed-forward system, for example, where the animal makes a voluntary movement such as a jet propelled escape, the efferents can be used to suppress, peripherally, the massive input from the statocysts that may saturate the afferent system. This could also be achieved centrally by an efference copy mechanism, as has been proposed for fish electroreception (Bell, 1981). Additionally, the system may operate in a feedback mode, whereby the afferent input feeds back through the efferents to dynamically adjust the sensitivity of the system (Williamson, 1986). This may be important in sustained swimming or in movements imposed by external water currents. Where the efferents are acting at the periphery, the frequency response of the system may well be limited by the conduction velocities of the efferents. The efferent axons are small, unmyelinated fibers (Budelmann *et al.*, 1987) and are likely to have much slower conduction velocities than the larger afferent fibers.

The statocyst afferents project to the ipsi- and contralateral lateral pedal, pedal, and ventral magnocellular lobes within the suboesophageal mass of the octopus brain (Budelmann and Young, 1984; Plän, 1987). Probably, the sensitivity of the sensory system can be improved centrally by summing multiple afferent inputs. For example, where ipsi- and contralateral statocyst inputs are from receptors responding to the same direction of movement, then these multiple channel inputs could be combined to improve the sensitivity of the system or to reduce the noise in the system (Aidley, 1971). This could also occur at the periphery, where some afferent neurons, in both crista and macula, receive multiple inputs from a number of nearby hair cells (Colmers, 1981; Budelmann *et al.*, 1987).

Future research

The idea of being able to predict the locomotory performance of a cephalopod solely from the morphology of its statocysts is very attractive, especially because all but a few species are unavailable for free swimming studies or for physiological testing. However, although such prediction based on a study of the vestibular system is now feasible for vertebrates, only generalized statements can be made about cephalopods.

There are two main reasons for this. First, there is no hydrodynamic model of endolymph flow within the statocyst that takes into account the special features of the statocysts. Although vertebrate semicircular canal models are a good starting point, we can have only limited confidence in the accuracy of predictions transported directly into the cephalopod domain. Second, there is no base of physiological work on cephalopods to provide the constants needed for a mathematical description of statocyst performance, or to test and refine any model predictions. For example, even the best model based on morphological studies, could not predict the effects of electrical coupling or motile cilia on the afferent response characteristics.

Future work, therefore, should be concentrated on developing an adequate model of statocyst endolymph flow, including a description of cupula movement. This should be complemented by an investigation of the afferent response characteristics of representatives of the different cephalopod groups. These data, together with a description of the swimming styles and the likely accelerations produced in a few species of cephalopods, should give us sufficient information to predict with some confidence the probable locomotory performance of an animal, based only on the morphology of its statocyst.

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